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SYSTEMATIC IMPLICATIONS OF COLOR PATTERN POLYMORPHISM IN *GONIOPSIS PULCHRA* (DECAPODA: BRACHYURA: GRAPSIDAE) FROM ECUADOR

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Abstract.—Three species in the genus *Goniopsis* de Haan are currently recognized: *G. pelii* Herklots, *G. cruentata* Latreille, and *G. pulchra* Lockington, found respectively along the coasts of tropical west Africa, the Caribbean, and the tropical east Pacific. Color pattern is used to distinguish between these species, with only minor morphological differences separating them. Specimens of *G. pulchra* collected from the coast of southern Ecuador were found to be variable in color. The overlap in color pattern phenotypes between some *G. pulchra* populations and *G. cruentata* suggests that both are subspecies of one American polytypic species, although hybridization between the two species or a sibling species-complex remain as less likely possibilities. Notes on the ecology and distribution of the color morphs are also presented.

Increased attention has been given recently to the importance of color pattern in the systematics of decapod crustaceans. Knowlton & Mills (1992), for example, have demonstrated that color morphs of several morphological species of alpheid shrimp represent reproductively isolated and biochemically distinct taxa and recognize that "color pattern holds enormous potential for defining species boundaries in this systematically difficult genus." The use of color patterns to differentiate among cryptic and sibling species in decapods may be applicable to the Brachyura as well (e.g., Williams & Felder 1986).

The grapsid genus *Goniopsis* de Haan (1833) consists of three sister species, *G. pelii* Herklots (1851), *G. cruentata* Latreille (1803), and *G. pulchra* Lockington (1876), which are distributed along the coasts of tropical west Africa, the Caribbean, and Pacific coasts of the tropical Americas, respectively. The three recognized species are virtually identical in morphology (e.g., gonopod structure) and are believed to constitute a species-complex of which two (*G. cruentata* and *G. pulchra*) are geminate (twin) forms. Rathbun (1918) and Manning & Holthuis (1981) differentiated the three species primarily on the basis of color pattern as this appeared to be species specific. While minor morphological differences (width of carapace, relative length of the dactylus and propodus of the fifth pereiopod, configuration of the anterior margin of the carapace, etc.) are stated to exist between the three species, the color patterns which allow the species to be distinguished are treated as diagnostic characters (Manning & Holthuis 1981). A description of the species-specific color patterns is presented in Table 1.

A collection of *G. pulchra* from southern Ecuador revealed considerable variation in color patterns. While no morphological differences (gonopod structure, width relative to length of carapace, ratio of fifth pereiopod dactylus length to propodus length, etc.) were noted, polymorphism in the color pattern of these crabs is described below with a dis-

Table 1.—Putative species-specific carapace color patterns of the three species of the genus *Goniopsis*. Color pattern descriptions are from Chace & Hobbs (1969) for *G. cruentata*, Rathbun (1918) for *G. pulchra*, and Manning & Holthuis (1981) for *G. pelii*. The geographic distribution of each species is also presented.

Species	*G. pelii*	*G. cruentata*	*G. pulchra*
Range	Atlantic: Tropical coast of west Africa	Atlantic: Bermuda, Bahamas and the Caribbean coasts	Pacific: Magdelena Bay, Baja, California to Peru
Carapace color pattern	Dark purple carapace with minute white spots. A conspicuous white stripe is present on the lateral margin of the carapace. Carinae on carapace with dark edgings.	Golden carapace with small purple spots giving a reticulated appearance. Distinct white circles with a dark red border on the lateral margin of the carapace. Transverse carinae on the carapace faint and unpigmented.	Purple-red carapace with irregular yellow or white spots. Distinct white circles with a dark red border on the lateral margin of the carapace. Transverse carinae on the carapace with dark edgings.

cussion of the potential systematic implications. Notes on the ecology and distribution of the color morphs are also presented.

Methods

Specimens of *Goniopsis pulchra* were collected using a large hand net or by hand and the coordinated effort of at least three people. A total of 55 specimens were captured at six collecting sites along the coast of southern Ecuador. The sites of collection were Puerto Exclusas, Guayaquil (02°15.7′S, 79°52.0′W; n = 2), San Pablo (02°08.5′S, 80°46.7′W; n = 9), Palmar (02°01.0′S, 80°44.1′W; n = 5), MonteVerde (02°02.7′S, 80°44.05′W; n= 11), Valdivia (02°56′S, 80°44.1′W; n = 15), and Rio Mancay, Olón (1°47.5′S, 80°45.4′W; n = 8). All of the specimens collected were adults belonging to both sexes with carapace width (cw) measuring from 25 to 46 mm. The color patterns of these specimens have remained quite stable in the preservative. The specimens discussed here have been deposited in the Division of Genetics and Physiology, Centro Nacional de Acuicultura e Investigaciones Marinas, San Pedro de Manglaralto, Ecuador.

Results

During three collecting trips (September 1991, January 1993 and October 1993), specimens of *G. pulchra* were collected exhibiting color patterns that did not fit the description for this species. For example, at two localities (Puerto Exclusas, Guayaquil City and Olón), two different color pattern morphs were observed and collected (Fig. 1). Specimens closely fitting the color description of *G. pulchra* (Table 1) were collected from burrows alongside a brackish-water lagoon of the Río Mancay, Olón, Ecuador (Fig. 1A). The carapace color pattern was purplish-red with widely spaced yellow spots very similar to the description of *G. pulchra* given by Rathbun (1918). (Wilson 1992, presents and agrees with the color pattern of the Olón specimens very well.)

In contrast, *Goniopsis* specimens collected from Puerto Exclusas, Guayaquil, Ecuador, displayed a color pattern distinctly different from the Olón specimens (Fig. 1B). The carapace of these crabs was golden with small purple reticulations (Fig. 1B) and matched the color pattern description of the Atlantic *G. cruentata* provided by Rathbun (1901, 1918) and the drawing presented in Chace & Hobbs (1969).

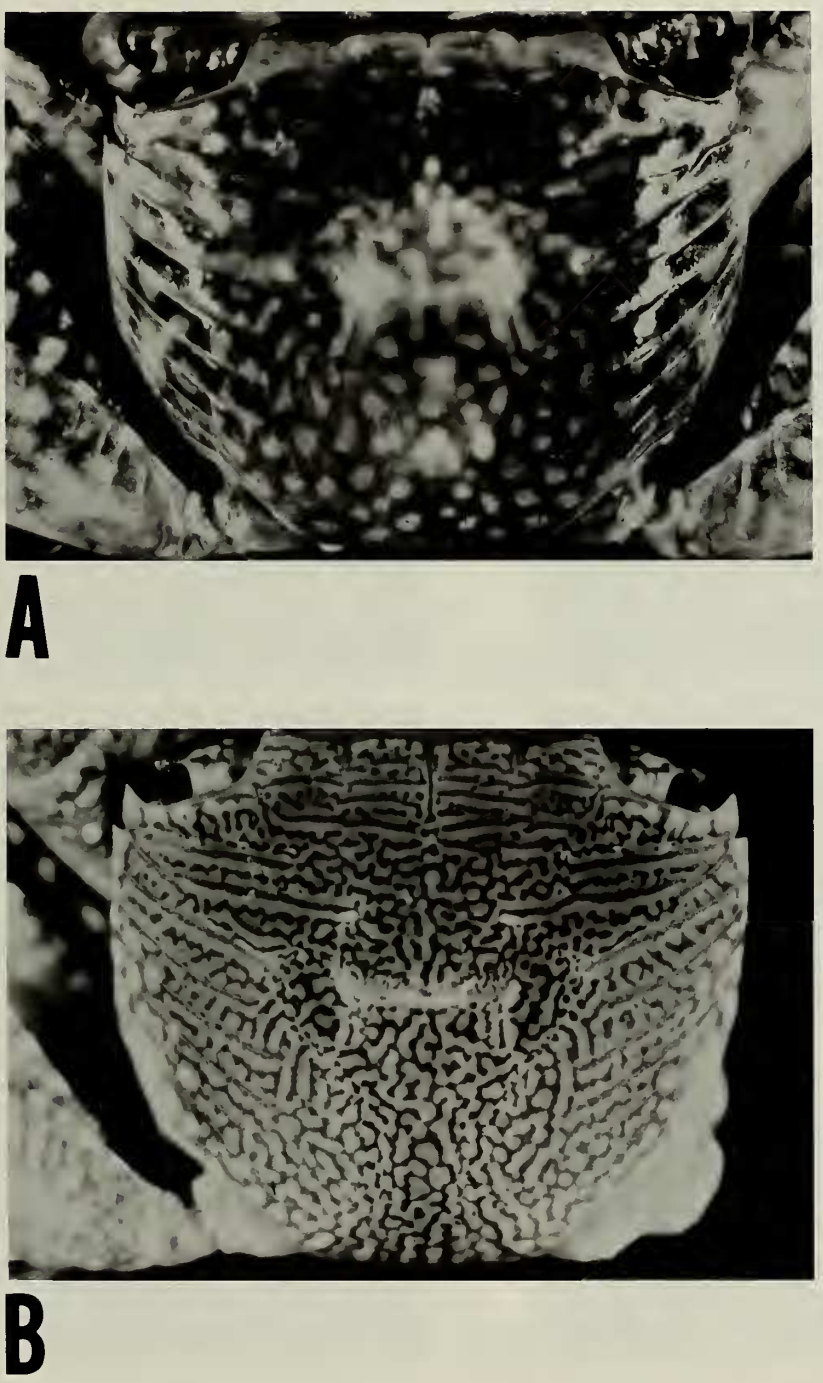

Fig. 1. Color pattern exhibited by two *Goniopsis pulchra* specimens collected from Olón, Ecuador (A), and Puerto Exclusas, Guayaquil, Ecuador (B). The specimen in A, a female (cw = 39 mm), displayed a dark purple-red carapace with widely spaced yellow spots. The front of the carapace in this specimen was bright red. The specimen in B, a male (cw = 32.5 mm), displayed a golden carapace with fine purple reticulations. The front of the carapace in this specimen was yellow.

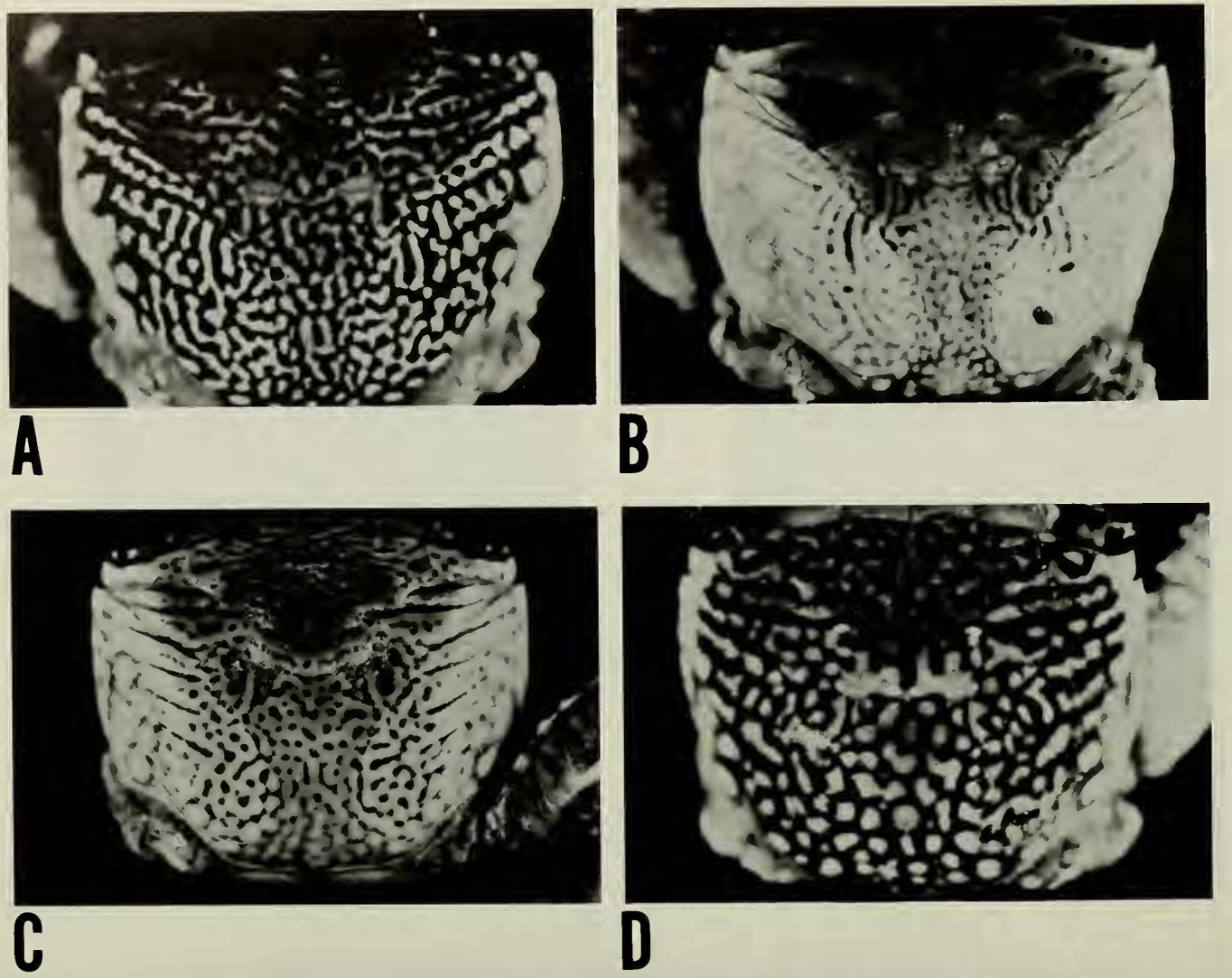

Fig. 2. Color pattern exhibited by *G. pulchra* specimens collected from a lagoon near MonteVerde, Ecuador. Coloration of the specimens are as follows: A, carapace color pattern intermediate between "*G. pulchra*" and "*G. cruentata*" specimens shown in Fig. 1 exhibited by a male (cw = 45 mm). The front of the carapace in this specimen was bright red. B, carapace color of a brilliant orange-yellow male (cw = 42 mm) with no carapace markings except for dark edgings on the transverse carinae. The front of the carapace in this specimen was a bright red. C, a female "*G. cruentata*" color morph (cw = 33 mm). The front of the carapace in this specimen was a bright red. D, a female (cw = 37 mm) "*G. pulchra*" color morph. The front of the carapace in this specimen was a bright red.

The "*G. pulchra*" and "*G. cruentata*" phenotypes were independent of the sex of the crabs.

A more complex array of color patterns was observed in the *G. pulchra* collected from an ecologically disturbed site near Monte Verde, Ecaudor. In an isolated saltwater lagoon fringed with mangroves, specimens were collected with color patterns intermediate between that of the "*G. pulchra*" and "*G. cruentata*" forms in addition to specimens with a different coloration (Fig. 2). One specimen had a color pattern intermediate between that of the specimens in Fig. 1 (Fig. 2A) and this specimen had a dark green-black carapace with large greenish-yellow blotches. Another specimen (Fig. 2B) was brilliant yellow-orange with very faint carapace markings. The color pattern of this individual was quite similar to that of brilliant red individuals also observed at this site. In addition, one specimen displayed a golden carapace with purple reticulations very similar to the "*G. cruentata*" specimen in Fig. 1B (Fig. 2C). A number of other specimens observed were more *G. pulchra*-like in appearance with the exception of the carapace ground color which was dark green-black and with the yellow spots less widely spaced (Fig. 2D).

The various morphs inhabiting the lagoon near Monte Verde were sympatric. Indeed, the four specimens in Fig. 2 were collected within ten meters of each other.

Morphological differences (e.g., gonopod structure) were not apparent between any of the *G. pulchra* specimens. However, one character used by Rathbun (1918) to differentiate *G. cruentata* from *G. pulchra* was carapace width. *Goniopsis cruentata* is described as having a carapace less broad than that of *G. pulchra*. In terms of this character almost all of the Eucadorian specimens can be established as *G. pulchra* with the exception of two individuals, which, while possessing a *G. pulchra*-like color pattern, have a square carapace (Fig. 2D).

Sampling of *G. pulchra* at six locations (see Materials and Methods) revealed geographic partitioning of color morphs which may be related to the ecology of the sampling sites. The *G. cruentata*-like morphs (Fig. 1B) comprise 100% of the population sampled in Guayaquil, San Pablo, Palmar, and Valdivia. The ecology of the sampling sites ranged from the mud banks and rubble of lagoons with little surrounding vegetation (Guayaquil, San Pablo and Valdivia) to the small mangrove forest of Palmar. The intermediate color morphs (Fig. 2A) predominated in Monte Verde (78% of the population) followed in number by the yellow-orange and red morphs (14%) and the "*G. cruentata*" morphs (7%). The MonteVerde site has approximately 20 mangrove trees fringing one region of a lagoon used for commercial salt production. Finally, the "*G. pulchra*" morphs have only been collected in the brackishwater marsh of the Río Mancay in Olón where they predominate and comprise 100% of the individuals collected. However, *Goniopsis cruentata*-like morphs have been observed in Olón. The "*G. pulchra*" morphs in Olón were found to be associated with the root complexes of trees and under logs whereas the *G. cruentata* morphs were observed to occupy burrows in the muddy shores of the lagoon.

Environmental factors which could possibly affect color and color pattern (e.g., food source, substrate, and time of mating) in the adults have been ruled out as laboratory populations from the six sampling sites have been maintained for up to six months with the specimen color patterns remaining constant throughout the moulting cycle.

Discussion

From a systematic point of view, the color pattern polymorphisms observed amongst *G. pulchra* collected from southern Ecuador raise serious questions about the status of *G. cruentata* and *G. pulchra* as distinct taxa. The most likely explanation for the color pattern variability observed is that *G.*

cruentata and *G. pulchra* are subspecies of one polytypic species (Mayr 1963). Gene complexes determining color pattern have been described in other crustacean species (reviewed in Hedgecock et al. 1982). It should be noted that approximately 95% of genes with visible effects in crustaceans involve polymorphisms in color or color pattern (Hedgecock et al. 1982). Extrapolating from the genetic data reviewed in Hedgecock et al. (1982), the "*G. cruentata*" and "*G. pulchra*" phenotypes described above for *G. pulchra* suggest the sharing of color pattern gene alleles between the two American species. An alternative explanation is that the color morphs are ecophenotypes resulting from environmentally dependent color pattern gene expression.

The overlap in color pattern between populations of *G. pulchra* from southern Ecuador and *G. cruentata* also extends to the west African *G. pelii*. *Goniopsis pelii* is characterized by "having small light spots on a purple background" (Manning & Holthuis 1981). The "*G. pulchra*" morphs are thus more similar in color pattern to *G. pelii* than to *G. cruentata*. The difference between *G. pelii* and *G. pulchra*, however, is the size of the carapace spots which are described as minute in the former (Manning & Holthuis 1981). Some juvenile "*G. pulchra*" morphs from Olón, nonetheless, have minute spots on a dark brown-purple carapace.

Manning & Holthuis (1981) mention a specimen of *G. cruentata* from Brazil with an atypical color pattern. While not describing the color pattern, this would suggest that Atlantic *Goniopsis* populations are also polymorphic for genes controlling color pattern. Rathbun (1918) does state that *G. pulchra* exhibits variability in terms of carapace blotching. Whether intermediate phenotypes constitute the "variability" Rathbun (1918) described is uncertain. It should be noted, however, that no intermediate color morphs were found in the alpheid shrimp sibling species-complex for which color pattern was used as a systematic indicator (Knowlton & Mills 1992).

With an increasing number of decapods being recognized as sibling and cryptic species (Knowlton 1986), it would be imprudent to argue for the conspecificity of *G. pulchra* and *G. cruentata* on color pattern polymorphism alone. A second possibility is that hybridization is taking place between *G. cruentata* and *G. pulchra*. With the exception of the broad "*G. pulchra*" frontal carapace, the color pattern of the specimen in Fig. 1B is identical to *G. cruentata* in almost every respect. Guayaquil is a large port city and *G. cruentata* larvae could have been transported from the Atlantic in ballast water. Should hybridization be taking place, the independent segregation of genes for color pattern and carapace width could well produce the color pattern combinations described here. However, the absence of distinct morphological differences between *G. pulchra* and *G. cruentata* prevents the unambiguous detection of hybrids on anatomical features alone.

A third, although less likely, possibility is that a *Goniopsis* species-complex exists in Ecuador. There is evidence that the *Goniopsis* color forms assortatively mate. At Olón and Valdivia, burrows of the land crab *Cardisoma crassum* were observed to contain pairs of crabs with one pair per burrow. A male and female will similarly share and protect a "burrow" (PVC pipe) in the laboratory. Hybridization between color morphs has nevertheless been observed under laboratory conditions.

There does appear to be geographic partitioning of the color morphs. The geographical partitioning may be the result of selection against brightly pigmented individuals in nonvegetated environments. Specimens from environments with vegetation (e.g., Monte Verde and Olón) were conspicuous in their coloration (brilliant red or yellow pigmentation) whereas crabs from nonvegetated sites were comparatively more

drab. The "*G. cruentata*" morphs were predominant at sites with no vegetation where their coloration was similar to that of the substrate. Juveniles (cw less than 20 mm) from all collection localities were a drab brown and cryptic in coloration.

Color pattern is polymorphic in many decapod species and this had led to taxonomic confusion (e.g., mangrove crabs of the genus *Scylla*; Estampador 1949). The polymorphisms observed in *Goniopsis* color pattern, purportedly a taxonomically significant indicator for this genus, suggest that the systematics of *Goniopsis* be reexamined. Color pattern, at least for *G. pulchra* from Ecuador, does not appear to be species specific. Manning & Holthuis (1981), referring to the differences between *G. cruentata* and *G. pelii,* state that a "closer study based on much more material and taking also the West American *G. pulchra* into account may establish that the three shoud be considered subspecies of a single species." The data presented here would support such a taxonomic revision of *Goniopsis.*

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